Cryptovaranoides is not a squamate

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Abstract.
Accurate reconstruction of the timescale of organismal evolution requires knowledge of the placement of extinct representatives among living branches. The fossil record has the capacity to reframe hypotheses of organismal evolution by producing representatives of clades that predate previously known fossils or node ages. Recently, one fossil with the potential to drastically change current consensus surrounding the timescale of reptile diversification was described from Triassic fissure-fill deposits in the United Kingdom. This taxon, *Cryptovaranoides microlanius*, was originally placed deep within the squamate crown clade, suggesting that many lineages of lizards and snakes must have appeared by the Triassic and implying long ghost lineages that paleontologists and molecular phylogeneticists have failed to detect using all other available data. Our team questioned this identification and instead suggested *Cryptovaranoides* had unclear affinities to living reptiles, but this alternative interpretation was again challenged by the

team that originally described this species. Here, we dissect the morphological character codings used to support a crown squamate affinity for *Cryptovaranoides microlanius* and illustrate empirical problems with analyses that hypothesize this taxon to be a crown squamate. Our analyses emphasize the importance of stringency in constructing hypodigms of fossils, particularly when they may be key for proper time calibration of the Tree of Life.

Keywords: *Cryptovaranoides,* Triassic, fossil, Squamata, Archosauromorpha.

Introduction.

Paleontology has found a new role in the era of widespread genome sequencing of living phylogenetic diversity: providing justification for the placement of fossil calibrations along molecular phylogenies [1–6]. Placing fossils on the Tree of Life has become common practice, and new discoveries [7–10] and reshuffling of hypothesized phylogenetic relationships [11] often revise which fossils are best to use as prior constraints. These factors make the robust placement of potential fossil calibrations essential for calibrating phylogenies to absolute time, which themselves are a foundation of modern evolutionary biology [12].

Recently, Whiteside et al. [13], described *Cryptovaranoides microlanius* based on a partially articulated skeleton and a collection of referred material from the Carnian [14] to Norian-Rhaetian [13,15–17] (237-201.5 million years ago) fissure fill deposits of England, UK. In a subsequent study, we [18] refuted the affinities of *C. microlanius* to Anguimorpha as a deeply nested crown squamate that was proposed by Whiteside et al. [13] based on a re-examination of the CT scan data of the holotype and referred specimens. This prompted substantial edits to how this taxon was scored in the morphological data matrix used to assess its phylogenetic relationships, finding *C. microlanius* to be "…*either an archosauromorph or an indeterminate neodiapsid*…" and not a lepidosaur, much less a crown squamate. In an impassioned response to our study, Whiteside et al. [19] disagreed with many of our anatomical observations and restated their position on the affinities of *C. microlanius.* Whiteside et al. [19] also referred additional Late Triassic fossils to *Cryptovaranoides microlanius* and presented putative phylogenetic results that this taxon is a crown group squamate (squamate hereafter).

Here we provide point-by-point re-examination of the new evidence and interpretations of Whiteside et al. [19] regarding the anatomy and phylogenetic affinities of *C. microlanius*. We identify and describe what we consider to be major methodological errors in the comparative anatomical work and phylogenetic analyses of Whiteside et al. [19], and present the results of our reanalysis of their actual data matrices and the recovered synapomorphies ignored by those authors.

Results.

Errors and Untested Synapomorphies

Both Whiteside et al. [13] and Whiteside et al. [19] include numerous comparative anatomy errors that can broadly be grouped into two categories: (i) anatomical interpretation, and (ii) translating these interpretations into scorings in different phylogenetic datasets. In Brownstein et al. [18], we identified 22 errors in the study of Whiteside et al. [13] of type (i) ("Results" in Brownstein et al. [18]) and several more of type (ii) ("Supplementary Material" in Brownstein et al. [18]). In Whiteside et al. [19], the authors claim that there were five observational errors in Brownstein et al. [18]. Four of these are supposed observational errors (type (i)) and one concerns a difference in how Brownstein et al. [18] and Whiteside et al. [19] score a character (type (ii)). In turn, this implies that Whiteside et al. [19] acknowledge that the other 18 type (i) errors produced by their previous study were correctly identified by Brownstein et al. [18]. Yet, Whiteside et al. [19] discuss additional characters in sections of their study and provide different interpretations of the anatomy of *Cryptovaranoides microlanius* than do Brownstein et al. [18], but without clear justification.

In this section we also revisit each alternative interpretation of the anatomy of *Cryptovaranoides microlanius* provided by Whiteside et al. [19], who discussed 26 characters that they suggest have bearing on the placement of this taxon within Lepidosauria, Pan-Squamata, crown Squamata, and successive clades within the crown. We note first that these characters do not correspond to optimized character states in the phylogenies that Whiteside et al. [13] and WEA24 inferred, but instead to an assemblage of character state optimizations presented in various papers in the literature (e.g., [20–22]). This is not an issue *per se* for a referral of *C. microlanius* to Squamata, but it does mean that these characters are of unclear relevance to the actual support for the position(s) of *C. microlanius* among reptiles that Whiteside et al. [13] and Whiteside et al. [19] recovered in the phylogenies that they presented. With this noted, we provide a point-by-point discussion of character interpretations in Brownstein et al. [18] that were challenged by Whiteside et al. [19].

Entepicondylar and ectepicondylar foramen of humerus. The features on the humeri that Whiteside et al. [19] figure and claim are the ente- and ectepicondylar foramina, are in fact, fossae that are filled in with sediment. Although they claim to observe this in yet another referred

humerus, they neither figure the internal structure of the bone nor provide any evidence for its referral to *Cryptovaranoides microlanius*. Contrary to the assertion of Whiteside et al. [19], CT scans do in fact provide essential information about the structure of these fossae and show that, when infill is removed, foramina are absent (Figure 4 in Brownstein et al. [18]). Further, these structures are in the wrong place to be the claimed foramina. In all diapsids that possess these foramina, they are placed low on the anterior surface (entepicondylar) and high on the distal surface (ectepicondylar) of the humerus (e.g., see [8,21] for examples in squamates, [23] for turtles, and [24,25] for sphenodontians) and are dissimilar in shape and size (the entepicondylar foramen is elongated along the long axis of the humerus; the ectepicondylar foramen is circular). The features that Whiteside et al. [19] figure are similar in shape and size, are placed on the same side of the bone, and differ in placement from humeral foramina observed in other exemplar fossils and living reptile species [8,21,23–25]. The morphology of the fossae observed on the distal end of the humeri referred to *C. microlanius* by Whiteside et al. [19] are, however, similar in placement, size, and shape to fossae described on the distal ends of the humeri of some archosauromorphs, including the azendohsaurid *Puercosuchus traverorum* (Figure 8; also see fig.13a in [26]). We further note that, even if WEA24's interpretation was accurate, the entepicondylar foramen is always absent in all crown squamates [8,21,27]. Among lepidosaurs, the presence of both entepicondylar and ectepicondylar foramina is found only among sphenodontians, stem lepidosaurs, and stem squamates [8,28]. Further, these foramina are also present in many non-lepidosaurian reptiles, including captorhinids (e.g. *Captorhinus*), younginiforms (e.g., *Hovasaurus* and *Youngina*), Claudiosaurus, Acleistorhinidae (Delorhynchus), *Mesosaurus*, the possible stem turtle *Eunotosaurus africanus*, and in some sauropterygians (e.g., *Serpianosaurus* and *Lariosaurus*)[8,29,30]. If anything, the presence of both foramina would support the assignment of *Cryptovaranoides* as outside of crown Squamata, not within the clade nor as a squamate synapomorphy. The position taken by Whiteside et al. [13] and Whiteside et al. [19] on this feature is puzzling.

Absence of jugal posterior process. WEA24 state: "*Except for a very few fossil taxa, including two polyglyphanodontians,Tianyusaurus and Polyglyphanodon, … squamates lack a posterior process on the jugal…*". This is entirely incorrect. The two extinct taxa noted by WEA24 here are only unusual among squamates in the fact that they have a complete lower temporal bar, and

thus an elongated jugal posterior process [21,31–33]. However, most families of squamates include species with a jugal posterior process (Figure 1)[8,21,22,32,34], even if a complete lower temporal bar is not present. The high degree of observed variability in the development of the jugal posterior process and lower temporal bar (e.g., Figure 1) means that the placement of *Cryptovaranoides microlanius* within any pan-lepidosaur clade based on this feature should be viewed with caution. The development and enclosure of the temporal fenestra in reptiles has been linked to the expression of two genes, *Runx2* and *Msx2*, in *in vivo* studies [35]. We suspect that the variable extent of this feature in many early-diverging lepidosaur and archosauromorph lineages might be an example of the 'zone of variability' [36], in which the canalization of development and other constraints (e.g., functionality; see [37]) had not yet completely acted to 'fix' the morphology of the posterior process. This hypothesis will of course require further experimental study of living model systems. Together, these observations suggest that the presence of a jugal posterior process was incorrectly scored in the datasets used by WEA24 (type (ii) error).

Anterior emargination of the maxillary nasal process. Whiteside et al. [19] state that Brownstein et al. [18] *"seemingly relied on the anteriorly broken left maxilla"* and that "*The anterior margin of the maxillary nasal process of the right maxilla tapers anteriorly…with no evidence of the type of emargination suggested"*. The character in question (ch. 18 in the dataset used by Whiteside et al. [19]), is one of the original characters from [8], which is the basis for the dataset used by Whiteside et al. [19] [38]. In both datasets, this character is described as "*Maxillae,* ***posterior emargination****, between nasal and orbital processes*"[boldface added], and this character is extensively described in [8]. Therefore, Whiteside et al. [19] incorrectly assessed the anterior margin of the maxilla instead of the posterior margin, which is another type (ii) error.

Expanded radial condyle of the humerus. Whiteside et al. [19] (p. 3) state that Whiteside et al. [13] "*noted an expanded radial condyle on the humerus.*" Yet, nowhere in Whiteside et al. [13] do the authors mention or figure such a structure. Whiteside et al. [19] (p.3, fig. 1b) write in their figure caption regarding another isolated fragment: *"(b) NHMUK PV 38911 isolated larger specimen of the distal end of left humerus of* Cryptovaranoides microlanius *in (above) anterior and (below) posterior views* ***showing similar features except the condyle of the capitellum.***"

(boldface added). Then, in Whiteside et al. [19] (subsection 2.3), the authors state that this fragment does not have a radial condyle/capitellum of the humerus, which they defend as follows: "*This is reinforced by the larger humerus (figure 1b) which is missing the condyle,* ***as is typical in the preservation of fissure lepidosaurs*** *(e.g. Clevosaurus; [12, fig. 29b]) but the* ***cavity in which it sat clearly indicates a substantial condyle in life.****"* (boldface added). What WEA24 highlight is that there is no condyle in this humerus or the holotype specimen and defer it to poor preservation without justification beyond *"…as is typical ….of fissure lepidosaurs…*" as a reason to conclude the condyle was present and to explain this inconsistency among the bones referred to *Cryptovaranoides.* Taphonomy and poor preservation cannot be used to infer the presence of an anatomical feature that is absent. Finally, even in the case of the isolated humerus with a preserved capitulum, the condyle illustrated by Whiteside et al. [19] is fairly small compared to even the earliest known pan-squamates, such as *Megachirella wachtleri* (Figure 4).

Preservation of the septomaxilla. Whiteside et al. [13] and Whiteside et al. [19] claim that a small, disarticulated piece of bone that is preserved anterolateral to the vomer in the block containing the holotype of *Cryptovaranoides microlanius* is the septomaxilla. They further suggest that a portion of the medial surface on a maxilla referred to this taxon that is likely from a much larger reptile provides additional support for the presence of a septomaxilla in *C. microlanius.* Simply put, the CT scans published by Whiteside et al. [13] and Whiteside et al. [19] show that the bone in the holotype is isolated and with no clear morphological affinities to the septomaxillae in squamates (see CT scans in [21]). Whiteside et al. [19] also suggest that the identity of this bone as the septomaxilla is supported by its placement between the maxilla and premaxilla of the holotype but given the level of disarticulation of the holotype and the morphology of the bone fragment, a similar argument could be made that it is a portion of the anterior end of one of the vomers. In any case, we feel it is premature to code *C. microlanius* for any character related to the morphology of the septomaxilla based on this disarticulated and damaged bone fragment.

Expanded radial condyle of the humerus. Whiteside et al. [19] provided additional justification of the presence of an expanded radial condyle of the humerus by stating that the projection of the radial condyle above the adjacent region of the distal anterior extremity of *Cryptovaranoides*

microlanius supports their choice to score the expanded radial condyle as present. This is not the condition specified in either of the morphological character sets that they cite [18,38] – the presence of a distinct condyle that is expanded – and is by their own description not homologous to the condition in other squamates.

Anterior emargination of the maxillary nasal process. Whiteside et al. [19] flagged our interpretation of the anterior maxillary nasal process as emarginated, which we found united *Cryptovaranoides microlanius* with archosauromorphs. Although we still interpret this state as such based on the computed tomography scan data, we again note than none of our analyses [18] unambiguously place *Cryptovaranoides microlanius* within Archosauromorpha and that, while optimized as such, this single character necessarily has limited utility for placing *C. microlanius* among reptiles.

Subdivision of the metotic fissure. Whiteside et al. [19] claim that the division of the metotic fissure into the vagus foramen and recessus scala tympani by the crista tuberalis, a key squamate feature, can be scored for *Cryptovaranoides microlanius*, yet paradoxically suggest the presence of this condition is only inferable based on other observations of the anatomy of the holotype and referred specimens. In fact, Whiteside et al. [19] argue that because another character relating to a different part of the structure of the metotic fissure can be inferred based on the presence of the crista tuberalis, that the division of the metotic fissure may also be inferred by the presence of the crista tuberalis. This logic would imply that no reptile taxon should exist that possesses solely either a crista tuberalis or a subdivided metotic fissure, even when this is an observed state combination in squamates scored for the matrices that both our teams have used to analyze the phylogenetic position of *Cryptovaranoides microlanius* [8,38]. Thus this inference lacks justification. To verify that *C. microlanius* possessed a vagus foramen, Whiteside et al. [19] state that they searched for isolated otoccipital fragments from the same locality and found an otoccipital fragment with a vagus foramen that they refer to *C. microlanius* without other justification. It is unclear to us how Whiteside et al. [19] accounted for confirmation bias when conducting this collections search, or on what basis they refer this isolated bone to *C. microlanius*. In any case, the presence of the lateral opening of the recessus scala tympani is not

figured in the fragment, and thus the division of the metotic fissure is not demonstrated in the referred fragment.

Fusion of exoccipitals and opisthotics. As Whiteside et al. [19] note, we concur with their identification of an otoccipital in *Cryptovaranoides microlanius* formed by the fusion of the exoccipitals with the opisthotics. Our concern is with the use of this feature to assign *C. microlanius* to Squamata. Whiteside et al. [19] cite de Queiroz and Gauthier [20], who list the presence of an otoccipital as a distinguishing feature of squamates. However, Whiteside et al. [19] fail to provide any phylogenetic evidence supporting the optimization of this feature as a squamate synapomorphy in phylogenies including *C. microlanius*, nor do they recognize that an otoccipital is present in numerous non-squamate reptiles, including numerous archosauromorphs [26,39,40]. For these reasons, the presence of an otoccipital alone cannot be used to assign *C. microlanius* to Squamata or even Lepidosauria instead of Archosauromorpha or other clades of reptiles known from the Permo-Triassic, except to distinguish the turtle total clade (*Eunotosaurus africanus* possesses unfused exoccipitals and opisthotics [41]). We acknowledge that with respect to a character state widespread among reptiles, optimization along a phylogeny is what is of primary importance for referring taxa to a particular clade. To this end, we reiterate that Whiteside et al. [19] did not show that the presence of an otoccipital optimizes as an ambiguous or unambiguous synapomorphy of Lepidosauria, Pan-Squamata, or Squamata in any of their phylogenies. For characters that show evidence of homoplastic evolution like the presence of an otoccipital (and indeed, the presence of a jugal posterior process; see above), phylogenetic character optimization is essential.

Enclosed vidian canal exiting anteriorly at base of each basipterygoid process. In our restudy of the holotype of *Cryptovaranoides microlanius*, we were unable to verify the presence of an enclosed vidian canal exiting the sphenoid via the base of the corresponding basipterygoid process. Whiteside et al. [19] take issue with our interpretation of this region of the braincase and suggest that a larger, abraded, and isolated sphenoid that they refer to *C. microlanius* also supports their interpretation of the anatomy of this region of the braincase. Yet, they stated that this fragment is of limited informativeness and appear to agree with us that the best course of

action is to score this character as missing data when including *C. microlanius* in phylogenetic analyses.

Development of the choanal fossa of the palatine. Squamata includes multiple instances where the complexity of the bony palate increases dramatically, an innovation that is related to chemosensory evolution and the integration of different bones that form this region of the skull [21,21,22,34,42–46]. One feature recognized as phylogenetically informative is the development of the choanal fossa on the ventral surface of the palatine (also known as the palatine sulcus) [18,21,34,47]. Whiteside et al. [19] claim that the development of the palatine choanal fossa in *Cryptovaranoides microlanius* is comparable to the development of this feature in living squamates, and cite the living iguanian genus *Ctenosaura* as an example of a squamate with similar anteroposterior development of this feature as *C. microlanius.* Importantly, most iguanians appear to show the plesiomorphic condition where the choanal fossa is anteriorly restricted on the palatine [21]; this feature has contributed to debates about whether Iguania forms the living sister group of all other crown squamates (as found in many morphological character-based phylogenies; [21,22]) or is deeply nested within the crown clade and secondarily convergent with rhynchocephalians (as implied by phylogenies made using DNA sequence data [48–54] and some made using morphological data [8]). As such, this comparison is not salient to the discussion about whether the development of the choanal fossa in *C. microlanius* represents the squamate condition. Secondly, Whiteside et al. [19] take issue with our contention that the palatine fossa is present, albeit variably, across a wide swath of reptilian diversity, including many early-diverging archosauromorph clades. They explicate this concern by distinguishing between the narrow channel found in taxa like *Tanystropheus* (figure 11 in Whiteside et al. [19]) and the wider fossa found in *C. microlanius*. We agree that the fossa in *C. microlanius* is more developed than in some early-diverging lepidosaurs, such as *Marmoretta oxoniensis* [55]. However, it is clear that the feature in *Cryptovaranoides* falls within the variation in the choanal fossa length and depth (Figure 2; Figure 3) that represents the ancestral condition in lepidosaurs [21] and is exemplified across archosauromorph (see, for example [26]) and indeed diapsid [56–58] diversity. Finally, Whiteside et al. [19] cite the discovery of a large, isolated palatine that they state confirms the presence of a “squamate-type” choanal fossa in *C. microlanius*, except they

provide no justification for why this isolated bone should be referred to this species. In any case, the morphology of that bone is also unlike those of squamates (Figure 2).

Vomer ventral ridges and dentition. Whiteside et al. [19] reiterated their earlier characterization [13] of the vomer of *Cryptovaranoides microlanius* as ridged, and suggest that the morphology of the vomerine ridges and vomerine teeth in *C. microlanius* is comparable to the condition in the anguid anguimorph *Pseudopus apodus*. We dispute this on the basis that the vomer of *C. microlanius* as figured by Whiteside et al. [19] shows no clear ridges equivalent to those in *Pseudopus apodus* [59] or other squamates with ridged vomers, including extinct forms such as *Eoscincus ornatus* [34] (Figure 4). Instead, the new photograph of the holotype specimen of *C. microlanius* provided in Whiteside et al. [19] shows that the vomer is indeed toothed, but no ridges are figured or visible. We once again reexamined the CT scan data and failed to find any structure resembling the ridges present in some anguimorphs, although we acknowledge that the nature of the scan data (43 microns per segment) means that the vomer surface on the scan segmentations is coarse. In any case, no ridges equivalent in shape or size to those found in anguimorph squamates are present in the holotype of *C. microlanius.* The presence of teeth on the vomer is itself rare among squamates; only in the pan-scincoid *Eoscincus ornatus* [34] and some [59] anguid and varanoid [60] species are vomerine teeth documented. Whiteside et al. [13,19] appear to suggest that the presence of vomerine ridges and a row of vomerine teeth therefore allies *C. microlanius* with anguimorphs. The structure of the vomer in *C. microlanius*, however, is fundamentally unlike those of anguimorph squamates, which are elongate and possess pronounced ridges that are placed medially on the ventral surface of the main body of each vomer and each house only one row of teeth along their posterior third [59,61]. In contrast, the condition that Whiteside et al. [19] figure for *C. microlanius* shows multiple, parallel rows of vomerine teeth on either side of the vomer that run across the entire length of the bone. This morphology is even unlike that observed in the only squamate known where multiple vomerine tooth rows are present, *Eoscincus ornatus* [34] (Figure 4). In that species, all vomerine teeth are restricted to a raised surface at the posterior end of the ventral surface of the vomer main body [34]. Thus, Whiteside et al. [19] have provided no evidence that vomerine ridges are present in *C. microlanius*. We note again that vomerine teeth are widespread across neodiapsid diversity outside Squamata [62] and appear in many lineages of Triassic archosauromorphs.

Lacrimal arches dorsally over lacrimal duct and floors lacrimal duct with medial process posteriorly. We argued that this feature was unobservable in the holotype of *Cryptovaranoides microlanius* [18]. Whiteside et al. [19] dispute this by suggesting that the CT scan data does not reliably show the feature, and instead provide a photograph of the holotype skull that was stated to show this morphology (figure 2a-c in [19]). This figure shows no curvature to the lacrimal, which appears as a flat element, whereas an arch dorsally and a floor ventrally would indicate the presence of a foramen. Whiteside et al. [19] did not code this feature (dorsal arcuation of the lacrimal over the lacrimal duct, which is posteriorly floored by the medial process of the lacrimal) for *C. microlanius*, but still use it to refer *C. microlanius* to Anguimorpha based on optimization as a plesiomorphy of that clade in phylogenetic analyses that place *C. microlanius* within Anguimorpha. This appears to suggest that, despite never conducting an analysis where this feature is coded as 'present' for *C. microlanius*, Whiteside et al. [19] used the presence of the feature to ally *C. microlanius* with Anguimorpha, not as a recovered synapomorphy, but stating that it was so. This action would be an arbitrary unification of a species with a clade based on a selected character state and would deny the equal possibility that this character state is absent due to secondary reversal in *C. microlanius.* In sum, the use of lacrimal morphology to ally *C. microlanius* with anguimorphs is apparently not based on direct character state optimization, i.e., a test of congruence.

Distinct quadratojugal absent. The quadratojugal cannot be located in the holotype of *Cryptovaranoides microlanius* [13,19]. We argued that this might be due to postmortem disarticulation and damage to the skull, and also noted that a complete ontogenetic series would *ideally* be required to test whether the quadratojugal is modified throughout ontogeny [18]. Whiteside et al. [19] focused on our comment about the ideal situation of having an ontogenetic series for *C. microlanius* to assess the development of the quadratojugal, which we restate would be helpful to understand how this bone transforms through ontogeny given the complex restructuring to this region of the skull that occurs throughout the evolution of lepidosaurs [63]. However, Whiteside et al. [19] state "we argue based on juvenile and adult specimens and the absence of a quadratojugal facet on the quadrate." First, the region of the quadrate that would articulate with the quadratojugal is not preserved in the holotype of *C. microlanius*, so it is

impossible to tell whether a facet for the quadratojugal is present. Second, Whiteside et al. [19] fail to provide any justification for the referral of the isolated partial quadrate NHMUK PVR 37606 to *C. microlanius*. Third, Whiteside et al. [19] did not identify the quadratojugal facet on this isolated quadrate when they figure this bone; indeed, based on the figure the process that would have housed the quadratojugal facet is also missing from this quadrate (NHMUK PVR 37606). It is impossible to tell whether *C. microlanius* lacked a quadratojugal based on the current data. Instead, all that can be said is that a quadratojugal is not preserved in the holotype of *C. microlanius*, and the region housing the articular facet for the quadratojugal is not preserved in either the holotype or referred quadrate.

Pterygoid/quadrate overlap. Whiteside et al. [19] restate the interpretation of Whiteside et al. [13] that the pterygoid and quadrate have a short overlap in *Cryptovaranoides microlanius.* Whiteside et al. [19] only compared the morphology of the quadrate in *Cryptovaranoides microlanius*, which they agree is damaged, to the morphology present in rhynchocephalians, and suggest based on this comparison that their interpretation is correct. We restate that this is not possible to verify without more complete, articulated or semi-articulated palates assignable to *Cryptovaranoides microlanius* based on apomorphic character states and combinations.

Fusion of the premaxillae and single median tooth. Whiteside et al. [19] suggest that Brownstein et al. [18] incorrectly characterized the nature of fusion of the premaxillae into a single median element in *Cryptovaranoides microlanius.* However, we reiterate that no justification has been given in any paper [13,19] for referring these isolated premaxillae to *C. microlanius.* Whiteside et al. [19] focus on differentiating these isolated large premaxillae from the premaxillae of two other fissure fill lepidosaurs, *Gephyrosaurus bridensis* and *Diphydontosaurus avonis*, without considering the possibility that additional taxa are present in the assemblage. Scoring fused premaxillae as present for *C. microlanius* despite the presence of unfused, paired premaxillae in the holotype defines (1) ontogenetic character state transformations solely based on the relative size of the holotype and larger isolated bones referred without justification and (2) which character state among those present in ontogeny is the phylogenetically informative one. Defining both of these requires a robust ontogenetic series, which is not available for *C. microlanius* at present. Observations of the development of living squamates also suggest that

these larger fused premaxillae should not be referred to *C. microlanius.* In crown squamates with a median premaxilla, the premaxilla is invariably a single element upon first appearance very early in embryonic development [64–68]. In contrast, the holotype of *C. microlanius*, which is very clearly a juvenile and not an embryonic specimen, possesses paired premaxillae. The ontogenetic series that Whiteside et al. [19] suggest for *C. microlanius* therefore differs from any known squamate with a single median premaxilla.

Peg-in-notch articulation of quadrate with rod-shaped squamosal. Whiteside et al. [19] suggest that both our teams are in agreement about the presence of a peg-in-notch articulation between the quadrate and squamosal. We reiterate that we believe the presence of this type of articulation is unclear based on the available data for the holotype, as these bones are both damaged in the relevant sections and disarticulated (Figure 5).

Frontal underlaps parietal laterally on frontoparietal suture. Whiteside et al. [19] confirm that the presence of this feature in *Cryptovaranoides microlanius* is based on the morphology of a referred isolated frontal that they state matches the corresponding articular portion of the prefrontal in the holotype. However, we do not understand how this bone could possibly match the corresponding articular surface unless it was from the same individual or an animal of exactly the same size. Unless Whiteside et al. [19] were actually able to articulate these bones, it is unclear how this inference can be made. Finally, we note that the posterior process of the prefrontal is broken off in the holotype of *Cryptovaranoides microlanius.* In squamates and other lepidosaurs, this process abuts the lateral surface of the frontal along its anteroposterior axis. Several of us (C.D.B. and D.L.M.) worked to rearticulated the holotype of *Eoscincus ornatus*, which involved rearticulating the prefrontal and frontal. Rearticulating these bones is simply impossible without the complete posterior process of the prefrontal, as the orientation of this process must match the curvature of the lateral margin of the frontal. Because the isolated frontal is not figured in either paper by Whiteside et al. [13,19], it is impossible for us to verify whether this bone actually matches the corresponding articulation surface on the prefrontal in the holotype. In any case, we regard it a best practice to exclude this isolated frontal from discussions of the affinities of *C. microlanius*.

Medial process of the articular and prearticular. Whiteside et al. [19] revise their initial [13] characterization of the medial process and refer to it as 'rudimentary,' scoring it as unobservable. We determined that this process is absent [18] and offer no further comment besides that it appears the distinction between our interpretation of this feature and that of Whiteside et al. [19] is, as they explicate, largely arbitrary.

Bicapitate cervical ribs and cervical ribs with an anteriorly oriented process. Whiteside et al. [19] took issue with our characterization of the morphology of the cervical ribs in *Cryptovaranoides microlanius*, and compared the bicapitate morphology of the cervical ribs in *C. microlanius* to two anguimorph squamates, *Pseudopus apodus* and *Varanus* spp. However, the cervical ribs of *P. apodus* are not bicapitate, as shown by the very figure from [69] that Whiteside et al. [19] cited. Similarly, the ribs of *Varanus* are unicapitate, not bicapitate, as shown in [70]. We assume that Whiteside et al. [19] referred to the morphology of the cervical rib head in *P. apodus* because of the presence of a posterior process on the rib head [69]. This is not the bicapitate condition and is not homologous with the morphology of the cervical rib heads in either *C. microlanius* or archosauromorphs, where an anterior process is offset from the process formed by the capitulum and tuberculum [39,71]. We reiterate that the condition in *C. microlanius* is identical to that in archosauromorphs (figure 2c, figure 3 in [18]); the comparisons made by Whiteside et al. [19] are across non-homologous structures and result from a misinterpretation of cervical rib anatomy.

Cervical and dorsal vertebral intercentra. Whiteside et al. [19] suggest that we inferred the presence of cervical and dorsal intercentra in *Cryptovaranoides microlanius*; however, we did not propose this in our paper. In fact, Whiteside et al. [13] state in their original paper that there "are gaps between the vertebrae indicating that intercentra were present (but displaced in the specimen) on CV3 and posteriorly. Some images of bones on the scans are identified as intercentra" (p. 11, [13]). The statement in [19] consequently represents an incorrect attribution and an incorrect characterization of our reexamination, as we determined that no cervical and dorsal intercentra were preserved or present in the holotype. Whiteside et al. [19] justify their position that cervical intercentra are present in *C. microlanius* based on the morphology of another isolated bone that they refer to this taxon. In any case, the absence of dorsal intercentra is

not a distinguishing feature of squamates because several lineages of squamates, including lacertids, xantusiids, gekkotans, and the stem-squamate *Bellairsia gracilis* all possess cervical and dorsal intercentra [38,72,73].

Anterior dorsal vertebrae, diapophysis fuses to parapophysis. Whiteside et al. [19] concur with Brownstein et al. [18] that the diapophyses and parapophyses are unfused in the anterior dorsals of the holotype of *Cryptovaranoides microlanius*, and restate that fusion of these structures is based on the condition they observed in isolated vertebrae that they again refer to *C. microlanius* without justification. As such, this feature should not be scored as present for *C. microlanius.*

Zygosphene–zygantrum in dorsal vertebrae. Whiteside et al. [19] again claim that the zygosphene-zygantrum articulation is present in the dorsal series of *Cryptovaranoides microlanius* based on the presence of 'rudimentary zygosphenes and zygantra' in isolated vertebrae that they again refer to this species without justification. The structures that Whiteside et al. [19] label as the zygosphenes and zygantra (figure 3 in [19]) are clearly not, however, zygosphenes and zygantra, as the former is by definition a centrally located wedge-like process that fits into the zygantrum, which is a fossa on the following vertebra. The structures labeled zygosphenes and zygantra by Whiteside et al. [19] are the dorsal surfaces of the prezygopophyses and the medial margins of the postzygapophyses.

Anterior and posterior coracoid foramina/fenestra. Whiteside et al. [19] use isolated coracoids referred to *Cryptovaranoides microlanius* to support their claim that the upper 'fenestra' (foramen) of the coracoid in the holotype specimen is indeed a foramen. Confusingly, Whiteside et al. [19] label this feature as the 'primary coracoid fenestra' in their figure 3i-j, even though it is clearly the coracoid foramen. Whiteside et al. [19] appear to have confused the coracoid foramen, which is completely bounded by bone and placed inside the coracoid, with the coracoid fenestra, which is bounded *in part* by the coracoid (the coracoid margin is curved to form part of the bounding region in species with the coracoid fenestra) but also by the interclavicle (see figures in [18,21]. The coracoid fenestra is not contained within the coracoid. This feature is also not shown to be optimized as a pan-squamate synapomorphy in any phylogeny including *Cryptovaranoides microlanius* [13,19], so its bearing on the identification of *C. microlanius* as a

pan-squamate is unclear to us. Finally, we note here that Whiteside et al. [19] appear to have labeled a small piece of matrix attached to a coracoid that they refer to *C. microlanius* as the supracoroacoid [*sic*] foramen in their figure 3, although this labeling is inferred because only "suc, supracoroacoid [*sic*]" is present in their figure 3 caption.

Atlas pleurocentrum fused to axis pleurocentrum. Whiteside et al. [19] reiterate their claim that the atlas and axis pleurocentra are present in *Cryptovaranoides microlanius* based on their identification of an isolated, globose bone fragment as the atlas intercentrum, but provide no additional justification for this identification and refer the reader to their original paper for a figure of this bone [13], which is only visible on CT scans due to its entombment within the matrix that includes the holotype. To this end, Whiteside et al. [19] revise their initial interpretation of the what they identify as the preserved atlas-axis region, but again without any justification or figures detailing how they reidentified a bone fragment that they had initially believed was a cervical intercentrum as the atlas centrum and intercentrum 2. Thus, Whiteside et [19] do not provide any additional description of how they reidentified these bones or a figure illustrating their revised interpretation, and so we cannot comment on the strength of their revised interpretation. Again, we note that we were not able to identify the morphology of the atlas and axis with any confidence in the holotype of *C. microlanius*, and so we again believe any relevant characters should be scored as missing data for this taxon.

Midventral crest of presacral vertebrae. Whiteside et al. [19] appear to agree with our assertion that a midventral crest is not present on the presacral vertebrae [18]. We never challenged their scoring of keels on the caudal centra as missing data. Rather, we stated that keels are clearly present on the cervical vertebrae [18].

Angular does not extend posteriorly to reach articular condyle. Whiteside et al. [19] state that the posterior portion of the angular is present medially on the right mandible in the holotype, and provide an interpretation of the anatomy of this region. They cite figure 3a in Whiteside et al. [19], but this shows the mandible in lateral view and only a small portion of the angular is visible. As such, it is not clear to us what they interpret to be the posterior portion of the angular. In any case, we could not identify anywhere on the CT scans or on the accessible portions of the

real specimen (e.g., figure 2b in [19]) the feature that Whiteside et al. [19] consider to be the posterior angular extent. Whiteside et al. [19] describe the posterior extent of the angular as a 'contoured feature,' but we are entirely unclear about what this actually describes.

Ulnar patella. The only disagreement between our interpretation [18] and that made by Whiteside et al. [13,19] concerns whether the ulnar patella is absent due to the ontogenetic state or preservation status of the holotype [13,19] or an ontogenetically invariable feature of the anatomy of *Cryptovaranoides microlanius* [18]; we suggested the latter based on our observation that the forelimb of the holotype is articulated and mostly complete.

Overarching Empirical Problems in Whiteside et al. [19].

Unassignable specimens and "hypodigm inflation." Whiteside et al. [13] and Whiteside et al. [19] describe and defend their addition of isolated elements to fill in gaps in the holotype concept of *Cryptovaranoides* to build, in our view, an unjustifiably inflated hypodigm. WEA24 (p. 15) try to ameliorate this problem in their Section (5.5) where they state that: "*We emphasize that we always match isolated bones with their equivalents on the holotype…*" and then state in contradiction that: "*We consider it* ***remiss*** *not to include isolated bones as they provide details which no scan can. Furthermore, as the holotype is a juvenile, they give additional information from larger, and presumably older individuals,* ***on characters of the holotype otherwise unavailable or uncertain***." (boldface added). In summary, Whiteside et al. [19] claimed to only match isolated bones with equivalent ones in the holotype but also acknowledged use of elements that are not comparable with the ones in the holotype. This lack of consistency is a serious empirical issue.

Apomorphic characters not empirically obtained. Whiteside et al. [19] discussed nearly 30 anatomical characters (Sections 2-6), most of which are used to support their core hypothesis that *Cryptovaranoides* is a squamate. Yet, none of these 30 characters or conditions are actually found by Whiteside et al. [19] to be synapomorphies of Squamata in their various phylogenetic analyses. In other words, they did not present the results of their Tests of Congruence, but rather simply elected to argue that untested interpretations of anatomy were apomorphies, synapomorphies, or shared characters.This is a non-trivial substantive methodological flaw in Whiteside et al. [13], that was perpetuated in Whiteside et al. [19], and that nullifies the bulk of the arguments presented repeatedly in both studies.

In Section 6, Whiteside et al. [19] (p. 16) indicate they modified the datasets of Brownstein et al. [18] and [38], but preferred the results of [11] and performed two different analyses based on [38]: one using only morphological data, and one using morphological data with several constraints from a molecular backbone. The former was tested using maximum parsimony and the latter using Bayesian inference. What is not clear from either Section 6 or 7, is which phylogenetic analysis was used by WEA24 to "*review the apomorphy distribution*". But this uncertainty is inconsequential as the apomorphy distributions discussed in Section 7 of Whiteside et al. [19] were not derived from their phylogenetic analyses. Instead, Whiteside et al.

[19] (p. 19) exclusively extracted characters from the literature to support their identification of *Cryptovaranoides* as a squamate, rather than basing this inference primarily on their own phylogenetic analyses. These literature sourced characters include *"two diagnostic characters of Squamata (=crown-clade Squamata)"* and *"…further eight squamate synapomorphies"* listed by WEA24 (Section 7, p. 19). As stated by the authors, "*we give the citation for the squamate synapomorphy at the end of each character"*— indicating that these diagnostic characters or synapomorphies were picked from the literature and not derived from ancestral state reconstructions based on their phylogenetic results.

In order to check the characters listed by Whiteside et al. [19] (p.19) as "*two diagnostic characters*" and "*eight synapomorphies*" in support of a squamate identity for *Cryptovaranoides*, we conducted parsimony analysis of the revised version of the dataset [38] provided by WEA24 in TNT v 1.5 [74]. We used Whiteside et al.'s [19] own data version—e.g., with (0) scored for character 1 and not including character 383. We recovered eight apomorphies at the squamate node of which only three were recovered as unambiguous synapomorphies (boldface indicates the state as scored by Whiteside et al. [19]for *Cryptovaranoides*):

Ch. 138. Basisphenoid (or fused parabasisphenoid), ventral aspect, shape, concavity: single (0)/divided (1)/ absent (**2**). 0 -> 2

Ch. 142. Prootics, alar crest: absent (0)/ present (**1**). 0->1

Ch. 347. Prefrontal/palatine antorbital contact: absent (0) / narrow forming less than 1/3 the transverse distance between the orbits (1) / contact broad, forming at least 1/2 the distance between the orbits (**2**). 01->2

The eight features described by Whiteside et al. [19] (p.19) as synapomorphies for *Cryptovaranoides* + Squamata were also not inferred at their recovered crown squamate node from their own results. Rather, they were copied nearly verbatim from principally two sources [21,75] and presented as if they were recovered as synapmorphies by Whiteside et al. [19] (p. 19). In Table 1, the italicized text is from Whiteside et al. [19] (p.19), including their literature source for the supposed synapomorphy. The non-italicized text is the character number and state from [11] as recovered by us from the TNT analysis conducted for this reassessment of Whiteside et al. [19]. We also include where in our phylogeny the character state is recovered as synapomorphic (Table 1).

Our reanalysis shows that Whiteside et al. [19] did not diagnose *Cryptovaranoides* + crown Squamata based on synapomorphies found by their own analyses as there were only three (see our results above). Instead, Whiteside et al. [19] provided ad hoc mischaracterizations of diagnostic features of crown Squamata from studies that did not include *Cryptovaranoides* and then discussed and reviewed synapomorphies of Squamata from these sources [21,75]. Because each additional taxon has the possibility of inducing character reoptimization, an empirical analysis of character optimization that includes a given new taxon is necessary to support referring said taxon to any particular clade. If *Cryptovaranoides* was indeed a Triassic crown squamate, it could plausibly show character distributions not previously sampled among known members of the crown or stem group.

Discussion and Conclusions.

As we noted above and in Brownstein et al. [18], the anatomy of *Cryptovaranoides* is similar to many Late Triassic neodiapsid reptiles. For example, the quadrates of *Cryptovaranoides* are closely comparable to those of archosauromorphs such as *Prolacerta* [76], *Macronemus* [77] and *Malerisaurus* [78], with which *Cryptovaranoides* shares the presence of a notch on the quadrate for an immobile articulation with the squamosal. Furthermore, WEA24's inference that the quadrate, the notch, and the articulation with the squamosal was mobile, i.e., streptostylic as in squamates, is unfounded.

Similarly, the vertebrae and cervical ribs of the holotype of *Cryptovaranoides* do not resemble those of squamates, but in fact share important features with non-squamate neodiapsids, especially archosauromorphs (a point left unaddressed by Whiteside et al. [19]). For example, whereas fusion of the neural arches to the centra occurs during embryonic ossification in squamates [79], in *Cryptovaranoides* unfused bony neural arches and centra are present, as commonly observed in archosaurs and other non-lepidosauromorph neodiapsids [80,81]—we provide a long-form review of these and other features in *Cryptovaranoides* that compare favorably with non-squamate reptiles in Supplementary Material.

Several errors in Whiteside et al. [13] identified in Brownstein et al. [18], and subsequent errors in Whiteside et al. [19] that were discussed above result in the incorrectly interpreted neodiapsid and lepidosaur anatomy of *Cryptovaranoides* and consequently provide erroneous scorings for *Cryptovaranoides* for morphological character matrices. Whiteside et al. [19] also

make additional errors on an alpha taxonomic level, such as the unjustified inflation of the *Cryptovaranoides* hypodigm based on contradictory arguments pertaining to the assignment of fragmentary and isolated elements to the holotype. Finally, we highlight here that where Whiteside et al. [13] and Whiteside et al. [19] should have reported their own recovered synapomorphies, that is, the actual results of their phylogenetic analyses, rather than listing a substantive number of supposed apomorphies that the authors argue support the squamate affinities of *Cryptovaranoides* broadly, and anguimorph affinities more specifically. On a methodological and analytical level, we do not consider that manually selecting apomorphic characters supporting their preferred placement of *Cryptovaranoides* instead of using characters empirically obtained from phylogenetic ancestral state reconstruction of their phylogenetic results, stands as valid support of a phylogenetic hypothesis.

We end with a perspective on the fossil record of neodiapsid evolution. The anatomies and morphologies that diagnose crown group squamates are many and varied, and except for a few features, hardly universally distributed amongst the living and fossil members of the crown. They are themselves the product of some 250 million years of evolutionary time and would not have evolved in a linear fashion. Rather, phylogenetic analyses of diverse extinct and living reptile clades have shown that the squamate *bauplan* originated in the context of extensive mosaic and homoplastic osteological character evolution [8,30,34,47,58]. We do not doubt that members of Pan-Squamata were present during the Triassic; this is supported by the fossil record [8] as well as numerous time-calibrated phylogenies based on genomic [48,49] morphological [34,38,47] and total-evidence [8,30] data. However, Whiteside et al. [13] and Whiteside et al. [19] have provided no direct osteological evidence that supports the presence of crown Squamata or any of its inclusive clades in the Triassic.

References

1. Inoue J, Donoghue PCJ, Yang Z. 2010 The Impact of the Representation of Fossil Calibrations on Bayesian Estimation of Species Divergence Times. *Syst. Biol.* **59**, 74–89. (doi:10.1093/sysbio/syp078)

2. Heath TA, Huelsenbeck JP, Stadler T. 2014 The fossilized birth–death process for coherent calibration of divergence-time estimates. *Proc. Natl. Acad. Sci.* **111**. (doi:10.1073/pnas.1319091111)

3. Near TJ. 2004 Estimating divergence times of notothenioid fishes using a fossil-calibrated molecular clock. *Antarct. Sci.* **16**, 37–44. (doi:10.1017/S0954102004001798)

4. Near TJ, Bolnick DI, Wainwright PC. 2005 Fossil calibrations and molecular divergence time estimates in centrarchid fishes (Teleostei: Centrarchidae). *Evolution* **59**, 1768–1782. (doi:10.1111/j.0014-3820.2005.tb01825.x)

5. Parham JF *et al.* 2012 Best Practices for Justifying Fossil Calibrations. *Syst. Biol.* **61**, 346–359. (doi:10.1093/sysbio/syr107)

6. Pennington PT, Cronk QCB, Richardson JA, Near TJ, Sanderson MJ. 2004 Assessing the quality of molecular divergence time estimates by fossil calibrations and fossil–based model selection. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **359**, 1477–1483. (doi:10.1098/rstb.2004.1523)

7. Field DJ, Benito J, Chen A, Jagt JWM, Ksepka DT. 2020 Late Cretaceous neornithine from Europe illuminates the origins of crown birds. *Nature* **579**, 397–401. (doi:10.1038/s41586-020-2096-0)

8. Simões TR, Caldwell MW, Tałanda M, Bernardi M, Palci A, Vernygora O, Bernardini F, Mancini L, Nydam RL. 2018 The origin of squamates revealed by a Middle Triassic lizard from the Italian Alps. *Nature* **557**, 706–709. (doi:10.1038/s41586-018-0093-3)

9. Brownstein CD. 2023 Syngnathoid Evolutionary History and the Conundrum of Fossil Misplacement. *Integr. Org. Biol.* **5**, obad011. (doi:10.1093/iob/obad011)

10. Velazco PM, Buczek AJ, Hoffman E, Hoffman DK, O'Leary MA, Novacek MJ. 2022 Combined data analysis of fossil and living mammals: a Paleogene sister taxon of Placentalia and the antiquity of Marsupialia. *Cladistics* **38**, 359–373. (doi:10.1111/cla.12499)

11. Budd GE, Mann RP. 2023 Two Notorious Nodes: A Critical Examination of Relaxed Molecular Clock Age Estimates of the Bilaterian Animals and Placental Mammals. *Syst. Biol.* , syad057. (doi:10.1093/sysbio/syad057)

12. Smith SD, Pennell MW, Dunn CW, Edwards SV. 2020 Phylogenetics is the New Genetics (for Most of Biodiversity). *Trends Ecol. Evol.* **35**, 415–425. (doi:10.1016/j.tree.2020.01.005)

13. Whiteside DI, Chambi-Trowell SAV, Benton MJ. 2022 A Triassic crown squamate. *Sci. Adv.* **8**, eabq8274. (doi:10.1126/sciadv.abq8274)

14. Simms MJ, Drost K. 2024 Caves, dinosaurs and the Carnian Pluvial Episode: Recalibrating Britain's Triassic karst 'fissures'. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **638**, 112041. (doi:10.1016/j.palaeo.2024.112041)

15. Walkden GM, Fraser NC, Simms MJ. 2021 The age and formation mechanisms of Late Triassic fissure deposits, Gloucestershire, England: Comments on Mussini, G. et al. (2020). Anatomy of a Late Triassic Bristol fissure: Tytherington fissure 2. *Proc. Geol. Assoc.* **132**, 127–137. (doi:10.1016/j.pgeola.2020.10.006)

16. Chambi-Trowell S, Whiteside D, Benton M. 2019 Diversity in rhynchocephalian Clevosaurus skulls basedon CT reconstruction of two Late Triassic speciesfrom Great Britain. *Acta Palaeontol. Pol.* **64**. (doi:10.4202/app.00569.2018)

17. Butler RJ, Meade LE, Cleary TJ, McWhirter KT, Brown EE, Kemp TS, Benito J, Fraser NC. 2024 Hwiccewyrm trispiculum gen. et sp. nov., a new leptopleuronine procolophonid from the Late Triassic of southwest England. *Anat. Rec.* **307**, 1390–1420. (doi:10.1002/ar.25316)

18. Brownstein CD, Simões TR, Caldwell MW, Lee MSY, Meyer DL, Scarpetta SG. 2023 The affinities of the Late Triassic Cryptovaranoides and the age of crown squamates. *R. Soc. Open Sci.* **10**, 230968. (doi:10.1098/rsos.230968)

19. Whiteside DI, Chambi-Trowell SAV, Benton MJ. 2024 Late Triassic Cryptovaranoides microlanius is a squamate, not an archosauromorph. *R. Soc. Open Sci.* **11**, 231874. (doi:10.1098/rsos.231874)

20. de Queiroz K, Gauthier JA. 2020 *Squamata*. CRC Press. See http://repository.si.edu/xmlui/handle/10088/107192.

21. Gauthier JA, Kearney M, Maisano JA, Rieppel O, Behlke ADB. 2012 Assembling the Squamate Tree of Life: Perspectives from the Phenotype and the Fossil Record. *Bull. Peabody Mus. Nat. Hist.* **53**, 3–308. (doi:10.3374/014.053.0101)

22. Estes R, de Queiroz K, Gauthier J. 1988 Phylogenetic relationships within Squamata. *Phylogenetic Relatsh. Lizard Fam.* , 119–281.

23. Hermanson G, Arnal FAM, Szczygielski T, Evers SW. 2024 A systematic comparative description of extant turtle humeri, with comments on humerus disparity and evolution based on fossil comparisons. *Anat. Rec.* **307**, 3437–3505. (doi:10.1002/ar.25450)

24. Simões TR, Kinney-Broderick G, Pierce SE. 2022 An exceptionally preserved Sphenodon-like sphenodontian reveals deep time conservation of the tuatara skeleton and ontogeny. *Commun. Biol.* **5**, 1–19. (doi:10.1038/s42003-022-03144-y)

25. DeMar Jr. DG, Jones MEH, Carrano MT. 2022 A nearly complete skeleton of a new eusphenodontian from the Upper Jurassic Morrison Formation, Wyoming, USA, provides insight into the evolution and diversity of Rhynchocephalia (Reptilia: Lepidosauria). *J. Syst. Palaeontol.* **20**, 1–64. (doi:10.1080/14772019.2022.2093139)

26. Marsh AD, Parker WG, Nesbitt SJ, Kligman BT, Stocker MR. 2022 Puercosuchus traverorum n. gen. n. sp.: a new malerisaurine azendohsaurid (Archosauromorpha: Allokotosauria) from two monodominant bonebeds in the Chinle Formation (Upper Triassic, Norian) of Arizona. *J. Paleontol.* **96**, 1–39. (doi:10.1017/jpa.2022.49)

27. Simões TR, Pyron RA. 2021 The Squamate Tree of Life. *Bull. Mus. Comp. Zool.* **163**, 47–95. (doi:10.3099/0027-4100-163.2.47)

28. Simões TR, Caldwell MW, Pierce SE. 2020 Sphenodontian phylogeny and the impact of model choice in Bayesian morphological clock estimates of divergence times and evolutionary rates. *BMC Biol.* **18**, 191. (doi:10.1186/s12915-020-00901-5)

29. Hill RV. 2005 Integration of Morphological Data Sets for Phylogenetic Analysis of Amniota: The Importance of Integumentary Characters and Increased Taxonomic Sampling. *Syst. Biol.* **54**, 530–547. (doi:10.1080/10635150590950326)

30. Simões TR, Kammerer CF, Caldwell MW, Pierce SE. 2022 Successive climate crises in the deep past drove the early evolution and radiation of reptiles. *Sci. Adv.* **8**, eabq1898. (doi:10.1126/sciadv.abq1898)

31. Simões TR, Funston GF, Vafaeian B, Nydam RL, Doschak MR, Caldwell MW. 2016 Reacquisition of the lower temporal bar in sexually dimorphic fossil lizards provides a rare case of convergent evolution. *Sci. Rep.* **6**, 24087. (doi:10.1038/srep24087)

32. Gao K, Norell MA. 2000 Taxonomic composition and systematics of Late Cretaceous lizard assemblages from Ukhaa Tolgod and adjacent localities, Mongolian Gobi Desert. *Bull. Am. Mus. Nat. Hist.* **2000**, 1–118. (doi:10.1206/0003-0090(2000)249<0001:TCASOL>2.0.CO;2)

33. Mo J-Y, Xu X, Evans SE. 2010 The evolution of the lepidosaurian lower temporal bar: new perspectives from the Late Cretaceous of South China. *Proc. R. Soc. B Biol. Sci.* (doi:10.1098/rspb.2009.0030)

34. Brownstein CD, Meyer DL, Fabbri M, Bhullar B-AS, Gauthier JA. 2022 Evolutionary origins of the prolonged extant squamate radiation. *Nat. Commun.* **13**, 7087. (doi:10.1038/s41467-022-34217-5)

35. Tokita M, Chaeychomsri W, Siruntawineti J. 2013 Skeletal gene expression in the temporal region of the reptilian embryos: implications for the evolution of reptilian skull morphology. *SpringerPlus* **2**, 336. (doi:10.1186/2193-1801-2-336)

36. Bever GS, Gauthier JA, Wagner GP. 2011 Finding the frame shift: digit loss, developmental variability, and the origin of the avian hand. *Evol. Dev.* **13**, 269–279. (doi:10.1111/j.1525-142X.2011.00478.x)

37. Schaerlaeken V, Herrel A, Aerts P, Ross CF. 2008 The functional significance of the lower temporal bar in Sphenodon punctatus. *J. Exp. Biol.* **211**, 3908–3914. (doi:10.1242/jeb.021345)

38. Tałanda M, Fernandez V, Panciroli E, Evans SE, Benson RJ. 2022 Synchrotron tomography of a stem lizard elucidates early squamate anatomy. *Nature* **611**, 99–104.

39. Ezcurra MD. 2016 The phylogenetic relationships of basal archosauromorphs, with an emphasis on the systematics of proterosuchian archosauriforms. *PeerJ* **4**, e1778. (doi:10.7717/peerj.1778)

40. Pinheiro FL, De Simão-Oliveira D, Butler RJ. 2020 Osteology of the archosauromorph Teyujagua paradoxa and the early evolution of the archosauriform skull. *Zool. J. Linn. Soc.* **189**, 378–417. (doi:10.1093/zoolinnean/zlz093)

41. Bever GS, Lyson TR, Field DJ, Bhullar B-AS. 2015 Evolutionary origin of the turtle skull. *Nature* **525**, 239–242. (doi:10.1038/nature14900)

42. Rieppel O, Kley NJ, Maisano JA. 2009 Morphology of the skull of the white-nosed blindsnake, Liotyphlops albirostris (Scolecophidia: Anomalepididae). *J. Morphol.* **270**, 536–557. (doi:10.1002/jmor.10703)

43. Lee MSY. 1997 The phylogeny of varanoid lizards and the affinities of snakes. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **352**, 53–91. (doi:10.1098/rstb.1997.0005)

44. Abramyan J, Richman JM. 2015 Recent insights into the morphological diversity in the amniote primary and secondary palates. *Dev. Dyn.* **244**, 1457–1468. (doi:10.1002/dvdy.24338)

45. Strong CRC, Scherz MD, Caldwell MW. 2022 Convergence, divergence, and macroevolutionary constraint as revealed by anatomical network analysis of the squamate skull, with an emphasis on snakes. *Sci. Rep.* **12**, 14469. (doi:10.1038/s41598-022-18649-z)

46. Watanabe A, Fabre A-C, Felice RN, Maisano JA, Müller J, Herrel A, Goswami A. 2019 Ecomorphological diversification in squamates from conserved pattern of cranial integration. *Proc. Natl. Acad. Sci.* **116**, 14688–14697. (doi:10.1073/pnas.1820967116)

47. Meyer D, Brownstein CD, Jenkins KM, Gauthier JA. 2023 A Morrison stem gekkotan reveals gecko evolution and Jurassic biogeography. *Proc. R. Soc. B* (doi:10.1098/rspb.2023.2284)

48. Title PO *et al.* 2024 The macroevolutionary singularity of snakes. *Science* **383**, 918–923. (doi:10.1126/science.adh2449)

49. Burbrink FT *et al.* 2020 Interrogating Genomic-Scale Data for Squamata (Lizards, Snakes, and Amphisbaenians) Shows no Support for Key Traditional Morphological Relationships. *Syst. Biol.* **69**, 502–520. (doi:10.1093/sysbio/syz062)

50. Townsend TM, Larson A, Louis E, Macey JR. 2004 Molecular Phylogenetics of Squamata: The Position of Snakes, Amphisbaenians, and Dibamids, and the Root of the Squamate Tree. *Syst. Biol.* **53**, 735–757. (doi:10.1080/10635150490522340)

51. Pyron RA, Burbrink FT, Wiens JJ. 2013 A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evol. Biol.* **13**, 93. (doi:10.1186/1471-2148-13-93)

52. Streicher JW, Wiens JJ. 2017 Phylogenomic analyses of more than 4000 nuclear loci resolve the origin of snakes among lizard families. *Biol. Lett.* **13**, 20170393. (doi:10.1098/rsbl.2017.0393)

53. Zheng Y, Wiens JJ. 2016 Combining phylogenomic and supermatrix approaches, and a time-calibrated phylogeny for squamate reptiles (lizards and snakes) based on 52 genes and 4162 species. *Mol. Phylogenet. Evol.* **94**, 537–547. (doi:10.1016/j.ympev.2015.10.009)

54. Singhal S, Colston TJ, Grundler MR, Smith SA, Costa GC, Colli GR, Moritz C, Pyron RA, Rabosky DL. 2021 Congruence and Conflict in the Higher-Level Phylogenetics of Squamate Reptiles: An Expanded Phylogenomic Perspective. *Syst. Biol.* **70**, 542–557. (doi:10.1093/sysbio/syaa054)

55. Griffiths EF, Ford DP, Benson RBJ, Evans SE. 2021 New information on the Jurassic lepidosauromorph *Marmoretta oxoniensis*. *Pap. Palaeontol.* **7**, 2255–2278. (doi:10.1002/spp2.1400)

56. Dudgeon TW, Maddin HC, Evans DC, Mallon JC. 2020 The internal cranial anatomy of Champsosaurus (Choristodera: Champsosauridae): Implications for neurosensory function. *Sci. Rep.* **10**, 7122. (doi:10.1038/s41598-020-63956-y)

57. Brownstein CD. 2022 High morphological disparity in a bizarre Paleocene fauna of predatory freshwater reptiles. *BMC Ecol. Evol.* **22**, 34. (doi:10.1186/s12862-022-01985-z)

58. Jenkins KM, Foster W, Napoli JG, Meyer DL, Bever GS, Bhullar B-AS. In press. Cranial anatomy and phylogenetic affinities of , with new information on the unique bolosaurid feeding apparatus and evolution of the impedance-matching ear. *Anat. Rec.* **n/a**. (doi:10.1002/ar.25546)

59. Klembara J, Dobiašová K, Hain M, Yaryhin O. 2017 Skull Anatomy and Ontogeny of Legless Lizard Pseudopus apodus (Pallas, 1775): Heterochronic Influences on Form. *Anat. Rec.* **300**, 460–502. (doi:10.1002/ar.23532)

60. Yi H-Y, Norell MA. 2013 New Materials of Estesia mongoliensis (Squamata: Anguimorpha) and the Evolution of Venom Grooves in Lizards. *Am. Mus. Novit.* **2013**, 1–31. (doi:10.1206/3767.2)

61. 2021 The anatomy, phylogenetic relationships, and autecology of the carnivorous lizard “Saniwa” feisti Stritzke, 1983 from the Eocene of Messel, Germany. *Comptes Rendus Palevol* **20**, 441–506.

62. Matsumoto R, Evans SE. 2017 The palatal dentition of tetrapods and its functional significance. *J. Anat.* **230**, 47–65. (doi:10.1111/joa.12534)

63. Ford DP, Evans SE, Choiniere JN, Fernandez V, Benson RBJ. 2021 A reassessment of the enigmatic diapsid Paliguana whitei and the early history of Lepidosauromorpha. *Proc. R. Soc. B Biol. Sci.* **288**, 20211084. (doi:10.1098/rspb.2021.1084)

64. Khannoon ER, Evans SE. 2020 Embryonic skull development in the gecko, Tarentola annularis (Squamata: Gekkota: Phyllodactylidae). *J. Anat.* **237**, 504–519. (doi:10.1111/joa.13213)

65. Hernández-Jaimes C, Jerez A, Ramírez-Pinilla MP. 2012 Embryonic development of the skull of the Andean lizard Ptychoglossus bicolor (Squamata, Gymnophthalmidae). *J. Anat.* **221**, 285–302. (doi:10.1111/j.1469-7580.2012.01549.x)

66. Skawiński T, Skórzewski G, Borczyk B. 2021 Embryonic development and perinatal skeleton in a limbless, viviparous lizard, Anguis fragilis (Squamata: Anguimorpha). *PeerJ* **9**, e11621. (doi:10.7717/peerj.11621)

67. Skawiński T, Kaczmarek P, Borczyk B. 2023 Embryonic development of the skull in a parthenogenetic lizard, the mourning gecko (Lepidodactylus lugubris). *J. Anat.* **243**, 618–629. (doi:10.1111/joa.13871)

68. Ollonen J, Da Silva FO, Mahlow K, Di-Poï N. 2018 Skull Development, Ossification Pattern, and Adult Shape in the Emerging Lizard Model Organism Pogona vitticeps: A Comparative Analysis With Other Squamates. *Front. Physiol.* **9**. (doi:10.3389/fphys.2018.00278)

69. Čerňanský A, Yaryhin O, Ciceková J, Werneburg I, Hain M, Klembara J. 2019 Vertebral Comparative Anatomy and Morphological Differences in Anguine Lizards With a Special Reference to Pseudopus apodus. *Anat. Rec.* **302**, 232–257. (doi:10.1002/ar.23944)

70. Cieri RL. 2018 The axial anatomy of monitor lizards (Varanidae). *J. Anat.* **233**, 636–643. (doi:10.1111/joa.12872)

71. Nesbitt SJ. 2011 The Early Evolution of Archosaurs: Relationships and the Origin of Major Clades. *Bull. Am. Mus. Nat. Hist.* **2011**, 1–292. (doi:10.1206/352.1)

72. Barbadillo LJ, Martínez-Solano I. 2002 Vertebral Intercentra in Lacertidae: Variation and Phylogenetic Implications. *Copeia* **2002**, 208–212.

73. Hoffstetter R, Jean. 1969 Vertebrae and ribs of modern reptiles. In: Gans, Bellairs and Parsons, Biology of the Reptilia. , 201–310.

74. Goloboff PA, Catalano SA. 2016 TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics* **32**, 221–238. (doi:10.1111/cla.12160)

75. de Queiroz K, Gauthier JA. 2020 Squamata. *Phylonyms Companion PhyloCode*

76. Modesto SP, Sues H-D. 2004 The skull of the Early Triassic archosauromorph reptile Prolacerta broomi and its phylogenetic significance. *Zool. J. Linn. Soc.* **140**, 335–351.

77. Miedema F, Spiekman SN, Fernandez V, Reumer JW, Scheyer TM. 2020 Cranial morphology of the tanystropheid Macrocnemus bassanii unveiled using synchrotron microtomography. *Sci. Rep.* **10**, 12412.

78. Nesbitt SJ, Stocker MR, Chatterjee S, Horner JR, Goodwin MB. 2021 A remarkable group of thick-headed Triassic Period archosauromorphs with a wide, possibly Pangean distribution. *J. Anat.* **239**, 184–206. (doi:10.1111/joa.13414)

79. Winchester L, Bellairs A d'A. 1977 Aspects of vertebral development in lizards and snakes. *J. Zool.* **181**, 495–525. (doi:10.1111/j.1469-7998.1977.tb03259.x)

80. Brochu CA. 1996 Closure of neurocentral sutures during crocodilian ontogeny: Implications for maturity assessment in fossil archosaurs. *J. Vertebr. Paleontol.* **16**, 49–62. (doi:10.1080/02724634.1996.10011283)

81. Griffin CT, Stocker MR, Colleary C, Stefanic CM, Lessner EJ, Riegler M, Formoso K, Koeller K, Nesbitt SJ. 2021 Assessing ontogenetic maturity in extinct saurian reptiles. *Biol. Rev.* **96**, 470–525. (doi:10.1111/brv.12666)

Figures

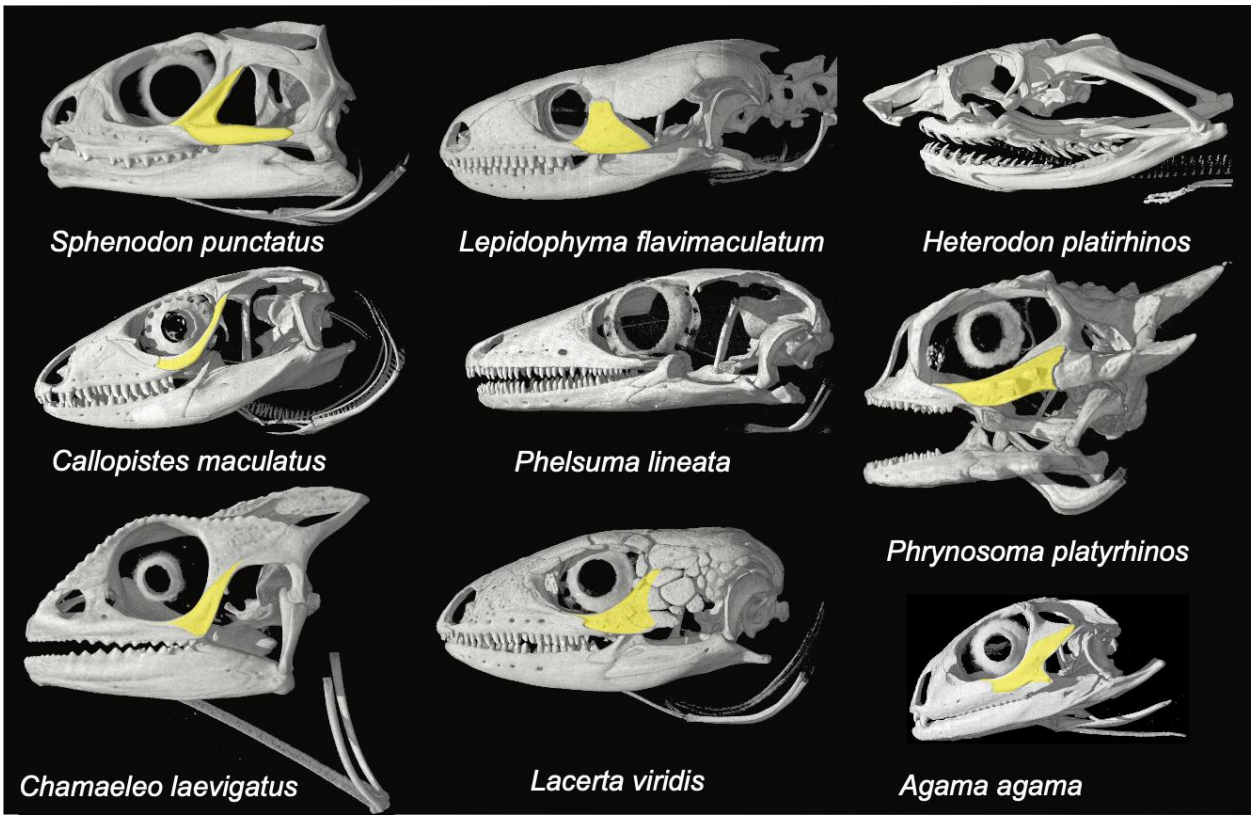


Figure 1. Comparison of jugal morphologies among living lepidosaurs. Note the variability in the presence and development of the posterior process, as well as the presence of an ossified jugal itself. CT scan images are from digimorph.org.

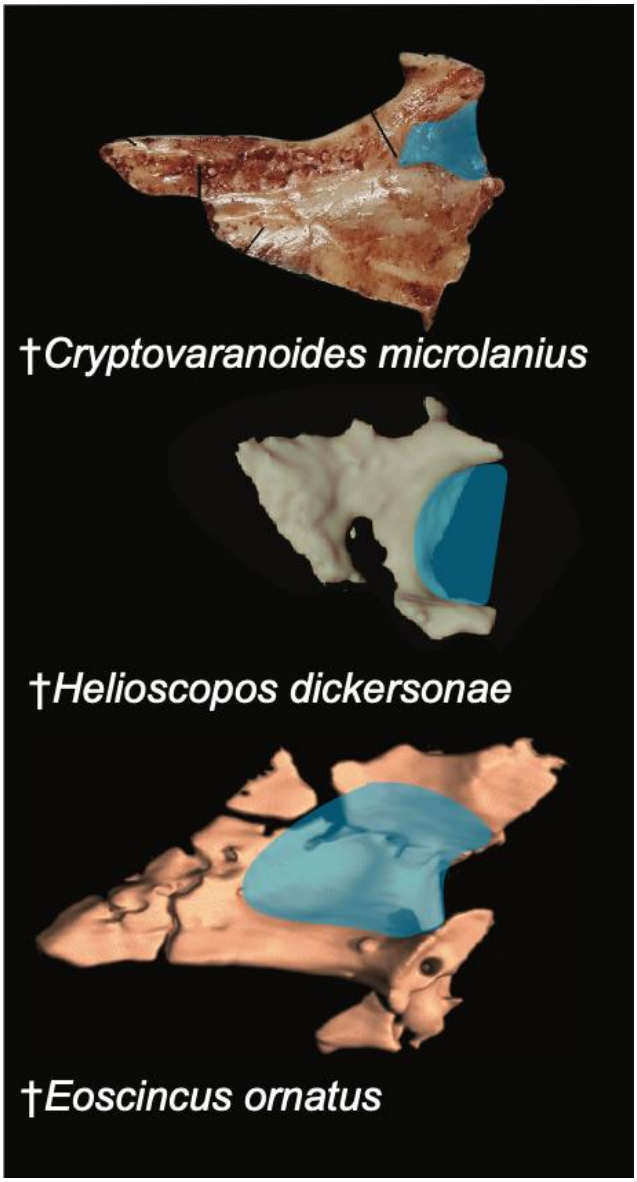


Figure 2. Comparison of palatine morphologies. Blue shading indicates choanal fossa. Top image of *Cryptovaranoides* referred palatine is from Whiteside et al. [19].

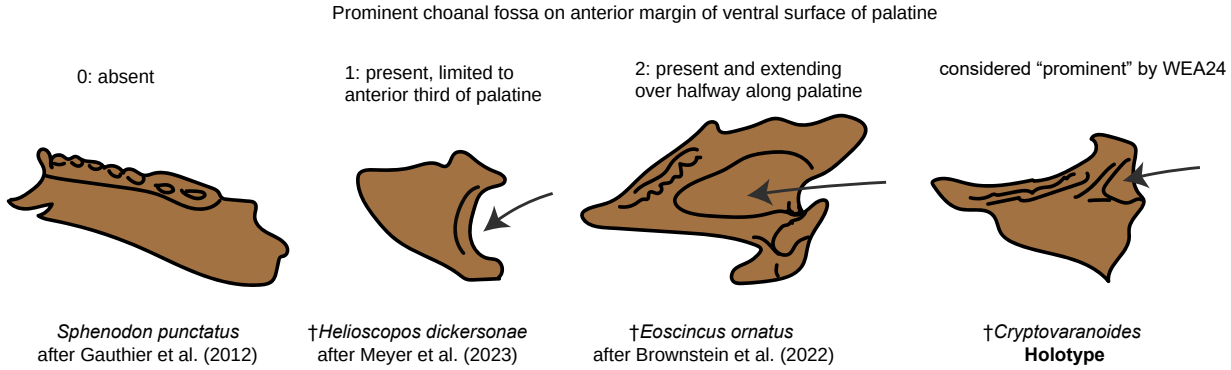


Figure 3. Choanal fossa character scoring.

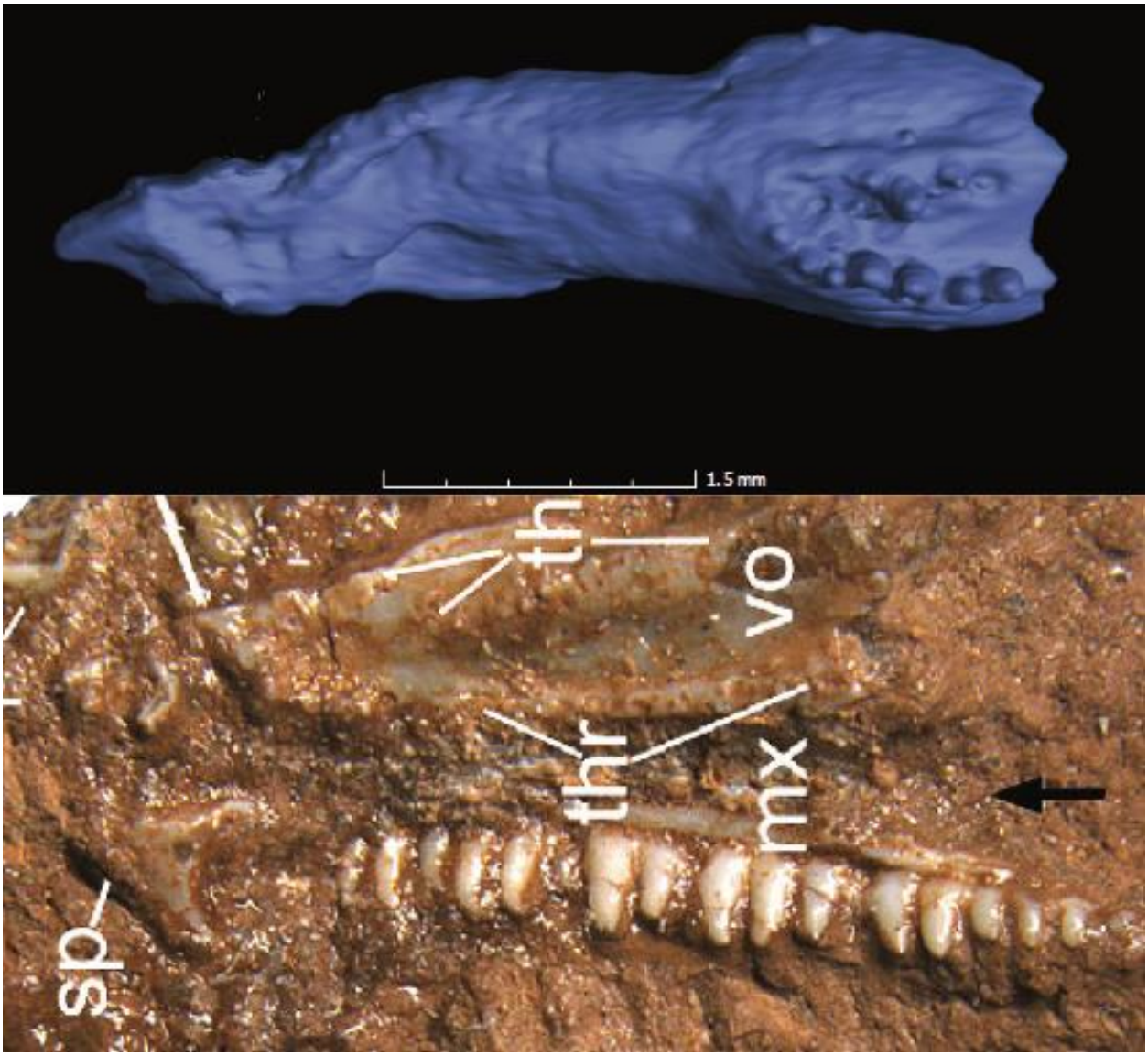


Figure 4. Comparison of vomer morphologies. Top image is *Eoscincus ornatus* from Brownstein et al. (2022). Note that the rows of vomerine teeth are posteriorly placed, and the vomerine ridges are large and laterally placed. Bottom image of *Cryptovaranoides* holotype is from Whiteside et al. [19].

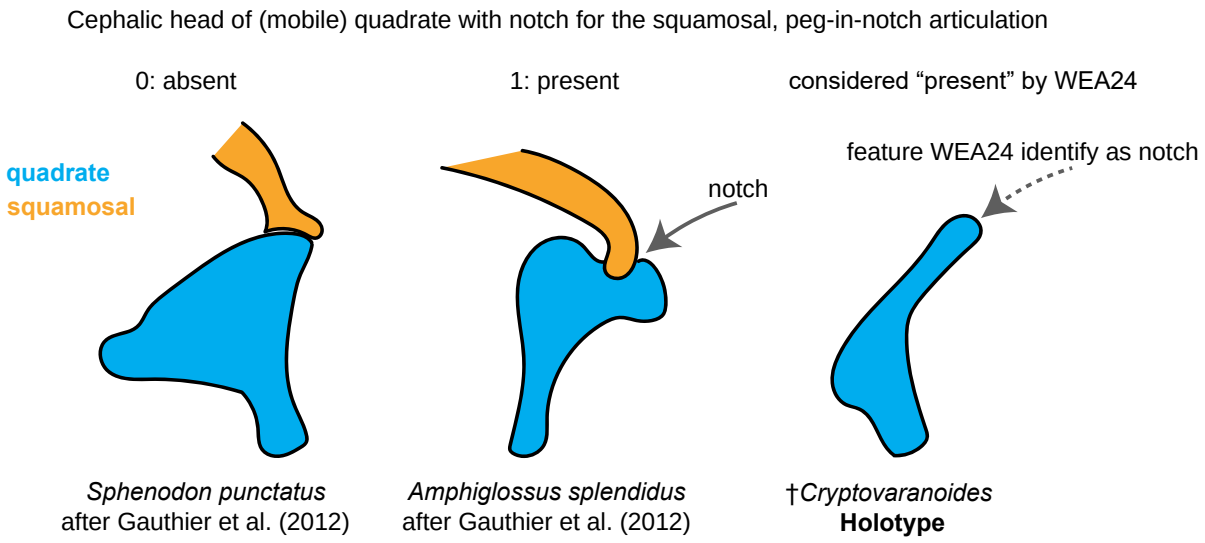


Figure 5. Quadrate-squamosal articulation character scoring.

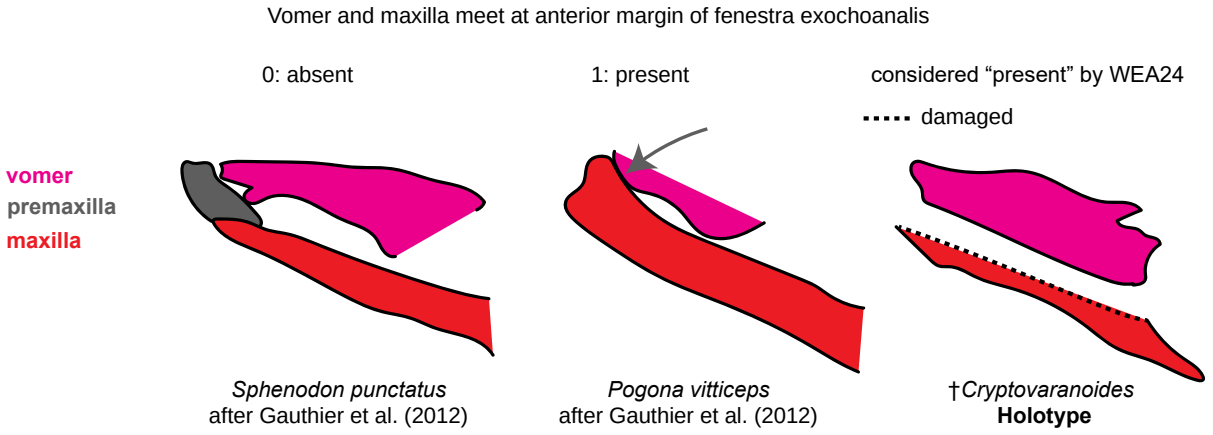


Figure 6. Anterior articulation of vomer and maxilla character scoring.

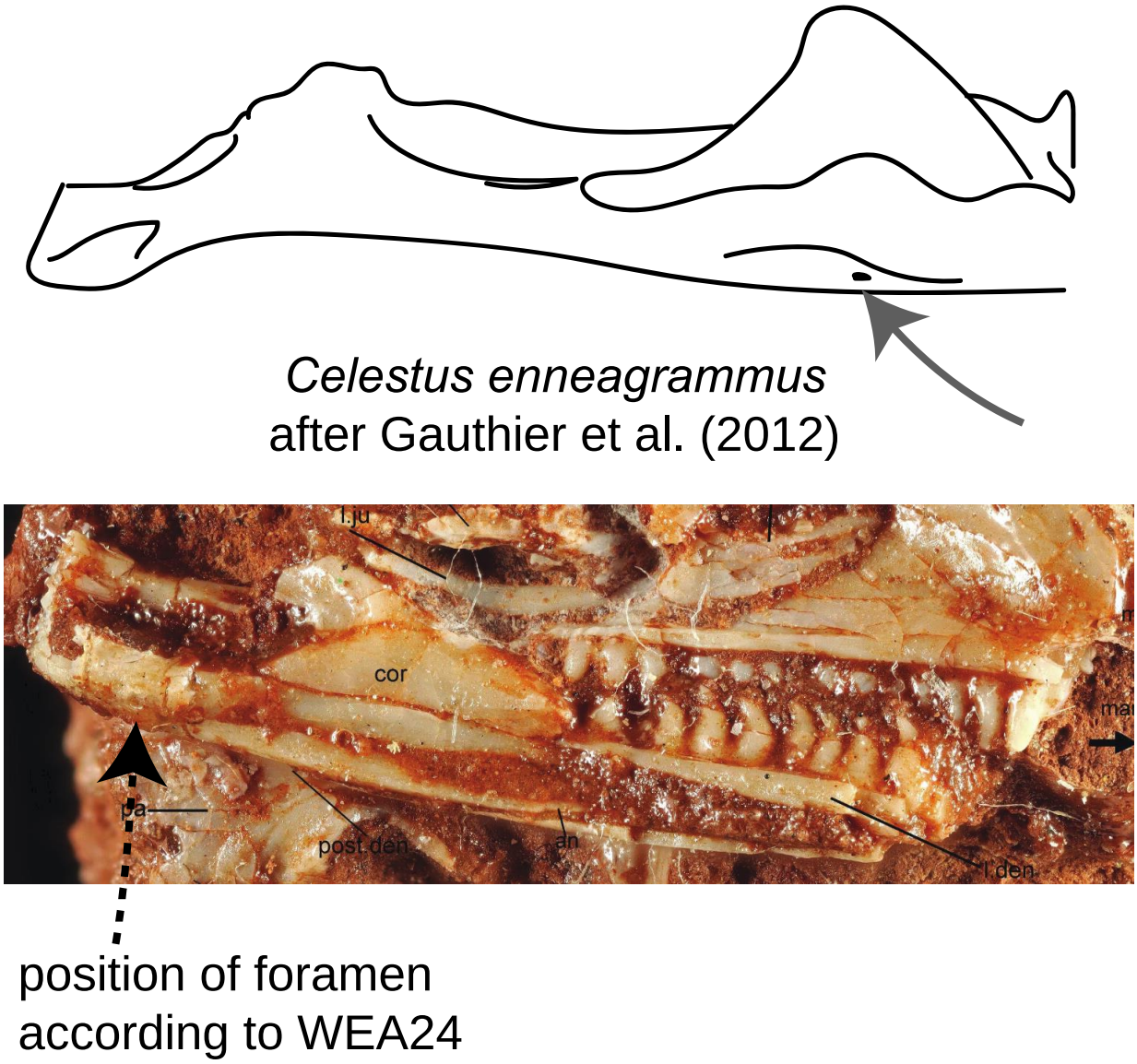
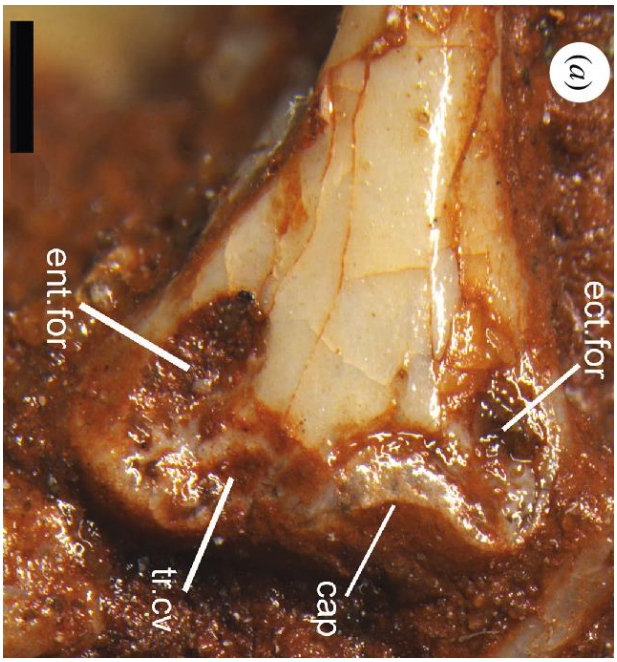
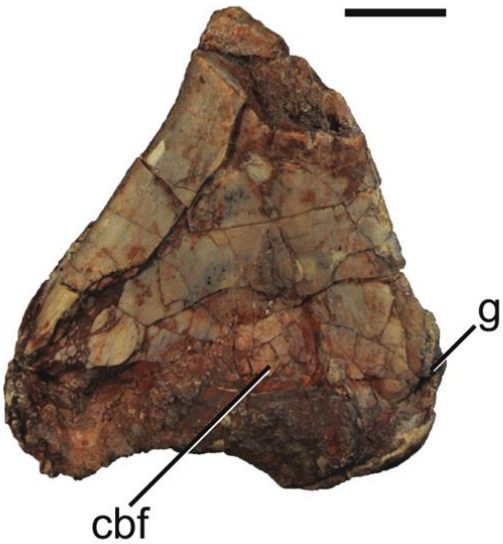


Figure 7. Presence of a medially positioned posterior mylohyoidal foramen on the mandible. As shown, there is no identifiable foramen on the mandible of *Cryptovaranoides*. Bottom image of *Cryptovaranoides* holotype skull is from Whiteside et al. [19].





†*Cryptovaranoides*
Holotype

†*Peurcosuchus traverorum*
after Marsh et al. (2022)

Figure 8. Comparison of the humerus of *Cryptovaranoides microlanius* to *Puercosuchus traverorum* [26]. Left image of *Cryptovaranoides* holotype humerus is from Whiteside et al. [19].

Table 1.

Character	Number in Talanda et al. (2022)	Study Cited in WEA24	Synapomorphy of	Unambiguous Optimization
Cephalic head of (mobile) quadrate with notch for the squamosal, peg-in-notch articulation with rod-shaped squamosal	123	de Queiroz and Gauthier (2020)	Pan-Squamata	1→0
Vomer and maxilla meet at anterior margin of fenestra exochoanalis	371	Gauthier et al. (2012)	N/A	N/A
Prominent choanal fossa on anterior margin of ventral surface of palatine	100	Gauthier et al. (2012)	Lepidosauria	N/A
Subdivision of embryonic metotic fissure by the crista tuberalis into vagus (jugular) foramen and recessus scala tympani	382	Simões et al. (2018); de Queiroz and Gauthier (2020)	N/A	N/A
No quadrate foramen	118	Gauthier et al. (2012)	Lepidosauria	1→0
Medially positioned posterior mylohyoidal foramen on mandible	163	Gauthier et al. (2012)	N/A	N/A
Fusion of exoccipitals and opisthotics forming an otoccipital	151	Gauthier et al. (2012); de Queiroz and Gauthier (2020)	N/A	N/A
Trunk vertebrae lack intercentra	237	de Queiroz and Gauthier (2020)	Pan-Unidentata	1→0